

Abstract—We investigated age, growth, and ontogenetic effects on the proportionality of otolith size to fish size in laboratory-reared delta smelt (*Hypomesus transpacificus*) from the San Francisco Bay estuary. Delta smelt larvae were reared from hatching in laboratory mesocosms for 100 days. Otolith increments from known-age fish were enumerated to validate that growth increments were deposited daily and to validate the age of fish at first ring formation. Delta smelt were found to lay down daily ring increments; however, the first increment did not form until six days after hatching. The relationship between otolith size and fish size was not biased by age or growth-rate effects but did exhibit an interruption in linear growth owing to an ontogenetic shift at the postflexon stage. To back-calculate the size-at-age of individual fish, we modified the biological intercept (BI) model to account for ontogenetic changes in the otolith-size–fish-size relationship and compared the results to the time-varying growth model, as well as the modified Fry model. We found the modified BI model estimated more accurately the size-at-age from hatching to 100 days after hatching. Before back-calculating size-at-age with existing models, we recommend a critical evaluation of the effects that age, growth, and ontogeny can have on the otolith-size–fish-size relationship.

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Modification of the biological intercept model to account for ontogenetic effects in laboratory-reared delta smelt (*Hypomesus transpacificus*)*

James A. Hobbs (contact author)^{1,2}

William A. Bennett^{1,2}

Jessica E. Burton¹

Bradd Baskerville-Bridges³

Email address for J. A. Hobbs: jahobbs@ucdavis.edu

¹ Bodega Marine Laboratory
2099 Westside Road
Bodega Bay, California 94923-0247

² John Muir Institute for the Environment
University of California, Davis
One Shields Ave.
Davis, California 95616

³ Department of Animal Sciences
University of California, Davis
One Shields Ave.
Davis, California 95616

Otolith-based back-calculation models of size-at-age rely on the assumption that the relationship between otolith and somatic growth is a constant proportion. This has often been examined by simply correlating otolith size with fish size for different aged fish. However, correlations of size among similarly growing body parts over time may not equate to proportional growth among these body parts (Cock, 1966). A comprehensive evaluation of the assumption of proportionality requires examining whether somatic variability is independent of age in the otolith-size–fish-size (OS-FS) relationship (Hare and Cowen, 1995). This requires an assessment of the residual variability between otolith size and fish size-on-age to remove the potential influence of age that can bias the OS-FS relationship (Hare and Cowen, 1995). Furthermore, the “growth effect,” where slow-growing fish have larger otoliths than fast-growing fish for similar-size fish, and the “ontogenetic effect,” where shifts in the OS-FS relationship occur, also need to be addressed before back-calculations. None of these proposed factors necessarily operate in isola-

tion and can occur simultaneously in multiple life stages (Hare and Cowen, 1995; Vigliola et al., 2000; Morita and Matsuishi, 2001). Therefore, before choosing an appropriate model for back-calculating size-at-age, it is necessary to identify the potential mechanisms responsible for variability in the OS-FS relationship.

Back-calculation models differ primarily in their ability to compensate for potential deviations away from a constant proportion between otolith size and fish size. The biological intercept (BI) model (for details on the model see Campana [1990]) compensates for growth effects by incorporating estimates of fish size and otolith size at the origin of the OS-FS proportionality. The time-varying growth (TVG) model adjusts the contribution of small and large increments with regard to body size (see Sirois et al. [1998] for full details), whereas the modified Fry (MF) model directly incorporates the allometric shape of the

* Contribution number 2313 from the Bodega Marine Laboratory, Bodega Bay, California 94923-0247.

relationship into the back-calculation model (for details see Vigliola et al. [2000]). Therefore, although these models can compensate for growth effects when age and ontogenetic effects are linked, they cannot provide accurate estimates when ontogenetic influences act independently of effects caused by growth and age. One means of compensating for ontogenetic shifts in the OS-FS relationship is to use the BI model separately for specific life stages. This model can be useful for providing accurate back-calculations across stage-specific transitions, such as metamorphosis (Jenkins, 1987; Campana, 1990; Otterlei et al., 2002).

We first assess whether the number of ring increments in otoliths accurately reflects absolute age in larvae and juvenile cultured (known-age) delta smelt (*Hypomesus transpacificus*). Second, we evaluate the degree to which age-independent variability occurs in the OS-FS relationship, as well as whether growth rate and ontogenetic effects modify the proportionality of otolith growth to fish growth. Finally, we modify the BI model to account for ontogenetic stage-specific transitions of the OS-FS relationship and compare these results with those from the TVG and MF models to assess the performance of our model for size-at-age back-calculations for delta smelt.

The delta smelt is a small osmerid fish endemic to the San Francisco Bay estuary (McAllister, 1963; Moyle, 2002). Historically one of the most common fishes, it was listed as “threatened” under the Federal and State Endangered Species Acts in 1993 (Moyle et al., 1992; USFWS, 1995; Sweetnam, 1999). Recent precipitous declines in the populations have led to a major investigation regarding the cause of such declines. A few of the potential sources include contaminants and exotic species (Bennett and Moyle, 1996; Bennett et al., 2005), both of which may result in reduced growth rates and poor recruitment. Examination of these hypotheses requires accurate estimates of back-calculated size-at-age for a growth-history assessment of the delta smelt (Fujiwara et al., 2005).

Materials and methods

Larval rearing and otolith examination

All known-age delta smelt larvae were reared at the University of California Davis’s delta smelt culturing facility located at the U.S. Bureau of Reclamation John F. Skinner fish facility in Byron, California. Newly hatched larvae were raised in 75-L black tanks at 20 larvae/L. Each tank maintained a flow-through system with filtered water from the Sacramento-San Joaquin delta. Ambient water temperatures during the rearing period ranged from 17° to 20°C and salinities from 0 to 1 ppt. The tanks were held in refrigerated cargo containers under 40-W florescent lights for a 12 h light:12 h dark cycle. Larvae up to 30 days after hatching (dah) were fed *Isochrysis* spp. enriched rotifers. *Nanochloropsis* spp. (green micro-algae) paste was added to create

“green” conditions necessary for larval feeding (Baskerville-Bridges¹; Baskerville-Bridges et al., 2004). Larvae more than 30 dah were fed *Artemia* sp. (brine shrimp) nauplii enriched in Super Selco® (Inve Aquaculture NV, Belgium). Ten larvae up to 10 dah were sacrificed daily with an overdose of MS222 (FINQUEL MS-222 Argent Chemical Laboratories, Inc., Redmond, WA) and fixed in 95% ethanol. Fish from 10 dah to 60 dah were sampled every other day and fish from 60 dah to 100 dah were sampled every 5–7 days (Table 1). Samples were collected from bins representing two spawning pairs of fish.

Sagittal otoliths were dissected from larvae and juveniles with fine forceps and dissecting needles. For larvae, care was taken to photograph and analyze only the sagittal otoliths, which were identified by orientation to the notochord. In delta smelt, the sagittal otoliths are located near the notochord, whereas lapilli are located distally and posteriorly in relation to the sagittae. Otoliths were mounted in Crystal Bond thermoplastic glue (Crystalbond™ 509, Ted Pella Inc. Redding, CA) with the sulcus side down. Otoliths from fish 92 dah and older were sanded with 1200-grit wet and dry sandpaper and polished with 0.3-micron alumina and a polishing cloth. Sagittal otolith radii were measured with a light microscope at 400–100× magnification. All otoliths were analyzed with Image Pro 4.0® (Media Cybernetics, Silver Spring, MD). The first increment was determined as the first ring after the nucleus core. Otolith radius was measured with the aid of image analysis, from the core to the dorsal edge, because this direction was consistently the clearest trajectory. All references to otolith size are radial measurements from the core to the dorsal edge. Sagittae were read by two readers without knowledge of fish age. Two readings were made by each reader and reread if age differences exceeded 10%. If age estimates continued to vary, the otolith was removed from the data set.

Statistical analyses

To determine if increment formation occurred on a daily basis, a Student’s *t*-test was used to determine the statistical significance of the slope from a linear regression of increment counts on known age. Under the null hypothesis, the slope of increment counts on known age was equal to one. We rejected the null hypothesis if the slope significantly differed from one.

Statistical analyses, similar to those of Hare and Cowen (1995), were used to evaluate age-independent variability in the OS-FS relationship, as well as growth rate and ontogenetic effects. First, regression models (linear and polynomial) of standard length and otolith

¹ Baskerville-Bridges, B. 2001. Progress and development of delta smelt culture: year-end report 2000. Interagency Ecological Program news letter 14:24–29. Department of Water Resources 827 7th St., Room 301, Sacramento, CA 95814.

Table 1
Summary of sample size, number of increment at designated days after hatching, and mean size-at-age.

Date	No. of Larvae sampled	Days after hatching	Mean no. of increments counted	Difference between days after hatching and mean no. of increments counted	Mean standard length (mm)
March 24	10	0	0	0	5.2
March 25	10	1	0	1	5.2
March 29	10	5	0.4	4.6	5.8
March 31	10	7	1.4	5.6	6.1
April 3	10	10	4.2	5.8	6.6
April 7	5	14	7.8	6.2	7.3
April 11	5	18	12.4	5.6	7.4
April 19	5	26	20	6	8.7
April 25	5	32	25.2	6.8	9.6
May 1	5	38	31.8	6.2	9.9
May 11	5	48	42.8	5.2	12.2
May 21	5	58	52.4	5.6	14.6
May 28	5	65	59.8	5.2	16.5
May 31	5	68	61	7	16.2
June 4	5	72	65.8	6.2	17.1
June 8	5	76	69.8	6.2	17.2
June 12	5	80	73.8	6.2	19.4
June 15	5	84	78.2	5.8	19.6
June 24	5	92	84.4	7.6	20.9
July 2	5	100	94	6	23.5

radius were regressed on age and otolith radius and age on standard length. Second, Pearson correlation coefficients of the otolith radius and standard length-on-age residuals were quantified to estimate the amount of age-independent variability. If no age-independent variability existed in the OS-FS relationship, the residuals of otolith radius-on-age and standard length-on-age should be perfectly correlated. The unexplained variability in the correlation between the residuals of the two models can be considered the degree to which age-independent variability can influence the OS-FS relationship. To account for growth rate effects, Pearson correlation coefficients were quantified for the residuals of age-on-length and otolith radius-on-length. Moreover, significant growth effects were detected with a positive correlation. Lastly, the slopes of the OS-FS relationship for each life stage were compared to account for ontogenetic effects. If otolith growth and fish somatic growth are in constant proportion throughout the life stages in question, the slopes between otolith-fish size should not be significantly different (Cock, 1966). The slope of otolith size to fish size was calculated with an allometric model of the form $y = ax^b$, where log transformation results in the formula $\log(y) = \log(a) + b \times \log(x)$ and the parameter b is equal to the slope (Gould, 1966).

Back-calculations

Size-at-age was back-calculated by using three models (Table 2). First, we examined the TVG model. This model accounts for variability in the underlying assumption of constant proportionality of otolith size to fish size by adjusting the contribution of increment widths by a growth factor. Second, we applied the MF model, which accounts for a nonlinear relationship between otolith size and fish size by directly estimating the shape parameters with a simple allometric model. Finally, a modified stage-specific form of the BI model was applied. Although this model depends on a constant proportion between otolith and fish size, we mediated this effect by applying the model to each specific life stage. To account for our stage-specific differences in the OS-FS relationship, we back-calculated size-at-age for the larval stage (5.4 mm SL to 12 mm SL) and juvenile stage (>12 mm SL) with 12 mm SL as the biological intercept. The mean back-calculated size-at-age trajectory was compared to measured standard lengths at time of sampling. We evaluated the fit of each model to the standard length-at-sampling data by comparing the r^2 values, as well as the minimum and maximum percent deviation of the mean back-calculated size-at-age value from the mean length-at-sampling.

Table 2

Summary of the three back-calculation models examined in this study: the time-varying growth (TVG) model (Sirois et al. 1998), modified Fry (MF) model (Vigliola et al. 2000), and the biological intercept (BI) model (Campana 1990). L =standard length; R =otolith radius; L_{op} =standard length-at-biological intercept; L_i =standard length-at-age i ; L_{cpt} =standard length-at-capture; R_{op} =otolith radius-at-biological intercept; R_i =otolith radius-at-age i ; R_{cpt} =otolith radius-at-capture; W =mean otolith increment width during each life stage; W_i =otolith increment width at i ; G_e =growth effect; and a =allometric shape parameter.

Back-calculation models	Equation	Reference
Time-varying growth (TVG)	$L_i = L_{op} + j(W_i + G_e(W_i - W))(L_{cpt} - L_{op})(R_{cpt} - R_{op})^{-1}$	Sirois et al. (1998)
Modified Fry (MF)	$L_i = a + \exp(\ln(L_{op} - a) + \ln(L_{cpt} - a) - \ln(L_{op} - a))$ $(\ln(R_i) - \ln(R_{op}))(\ln(R_{cpt}) - \ln(R_{op}))^{-1}$	Vigliola et al. (2000)
Biological intercept (BI)	$L_i = L_{cpt} + (R_i - R_{cpt})(L_{cpt} - L_{op})(R_{cpt} - R_{op})^{-1}$	Campana (1990)

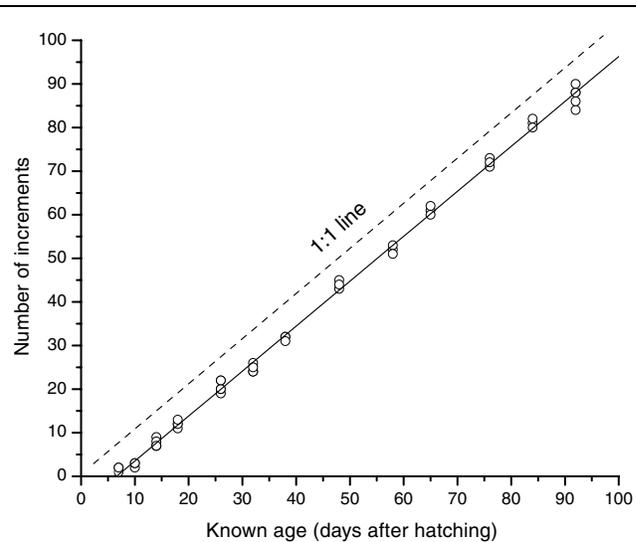
Results

Validation of daily otolith increment formation

The relationship between the number of increments and days after hatching of delta smelt larvae are shown in (Table 1; Fig. 1). The slope of the regression of increment count on known-age was not significantly different from one and thus indicated that increment formation occurred daily. However, the intercept was significantly different from zero ($P < 0.001$), indicating that the first increment was not laid at hatching, rather that ring formation began 6 dah. This observation was confirmed by examination of larvae sampled at one and five dah (Table 1).

Mean somatic and otolith growth

All somatic otolith-growth relationships were best described by life-stage-specific linear regression models, where larval (0–20 dah, 5–12 mm SL) and juvenile (>20 dah, >12 mm SL) life stages were considered separately. Calculated Akaike information criterion (Sokal and Rohlf, 1973) for the linear models were lower than polynomial models ranging from the 2nd to 9th orders. Somatic growth showed variations in growth over time: fast growth occurred from hatching to 40 dah, followed by a period of slowed growth from 40 dah up to 80 dah. After 80 dah, fish experienced a period of rapid somatic growth associated with the juvenile stage (Fig. 2, A and C). Otolith growth showed a different trend. Otolith growth was slow from hatching to 40 dah, which then increased exponentially from 40 dah to 100 dah, indicating that the relationship between otolith growth and fish growth changes abruptly around 40 dah with the completion of caudal flexing (Fig. 2B). Finally, the relationship between otolith size and fish size was best described by a stage-specific linear regression (Fig. 2D), which accounted for the lack of constant linear proportionality of otolith growth to fish growth. It is important to note that some patterns in the residuals were apparent in the early larval stages. However, we do

**Figure 1**

Relationship between the number of increments and the known age for delta smelt (*Hypomesus transpacificus*). Dotted line is the 1:1 ratio line. Solid line is the linear regression line.

not consider these slight deviations to have a significant effect on further residual analyses.

Growth and ontogenetic effects and size back-calculations

Correlations of age-independent effects and growth-rate effects are shown in Figure 3, A and B. The strong correlation between standard length-on-age residuals and otolith radius-on-age residuals may indicate that otolith size is proportional to fish size. The age-independent variability in the OS-FS relationship was accounted for by examining the unexplained variability in the residual analysis of otolith and fish size-on-age. Only 11% of the unexplained variability could be associated with age-independent effects. The Pearson correlation coefficient for the residual of standard length-on-age and otolith

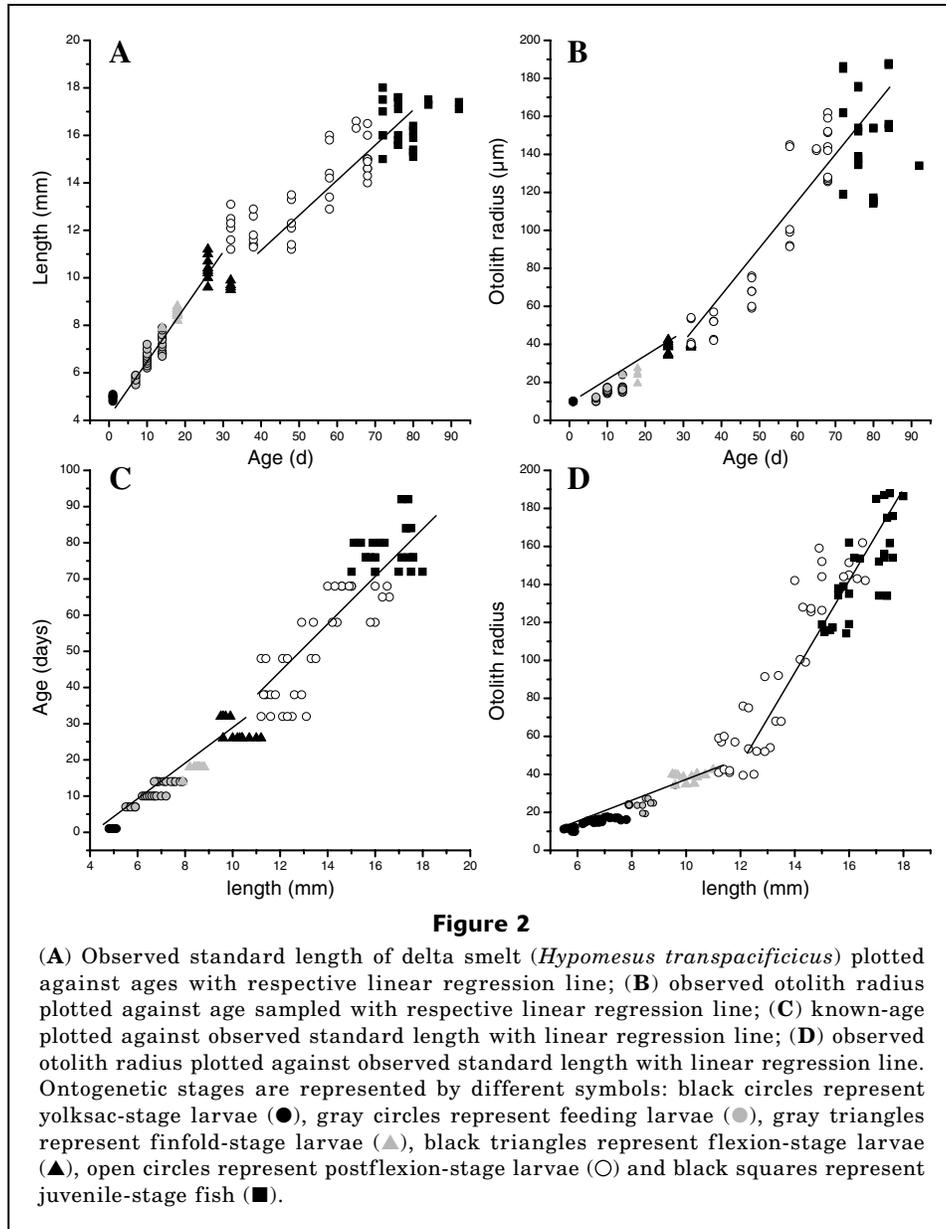


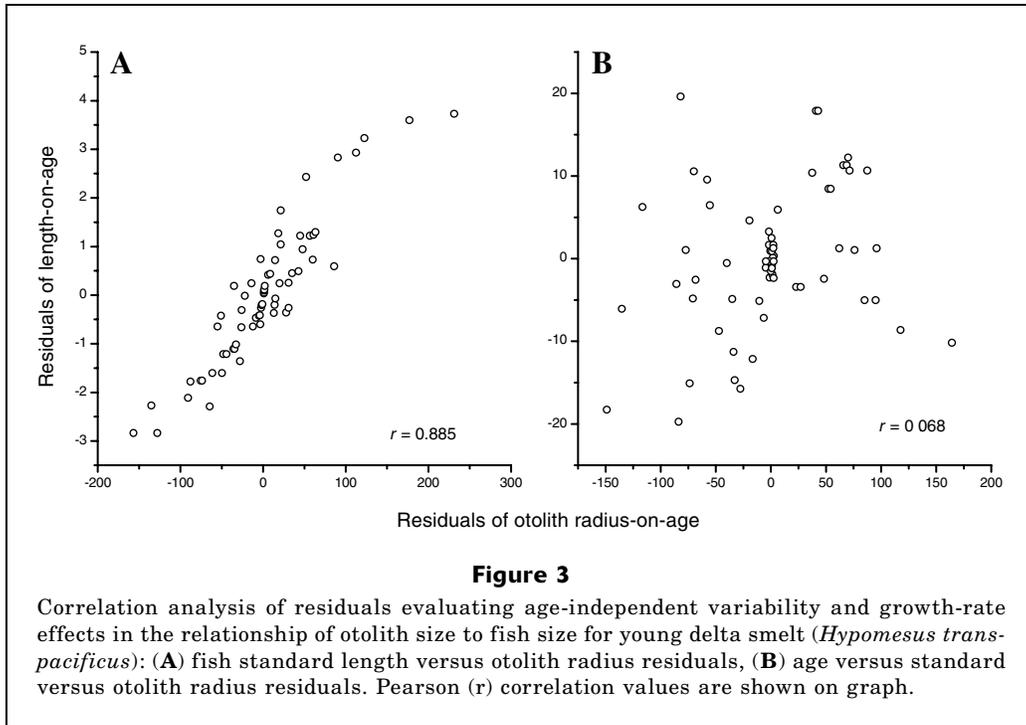
Table 3

Comparison of the allometric slope (*b*) values ($\log(\text{otolith radius}) = b \times \log(\text{standard length})$). *P* values are from Student's *t*-statistic.

Life stage	I	II	III	IV	V	VI
I	—					
II	<0.001	—				
III	<0.001	ns	—			
IV	ns	<0.01	<0.001	—		
V	<0.001	ns	ns	<0.001	—	
VI	<0.001	ns	ns	<0.001	ns	—

radius-on-age was 0.885 ($P=0.001$) (Fig. 3A). Comparison of the residuals of otolith radius-on-length and age-on-length demonstrated that there was no significant growth rate effect on the OS-FS relationship (Fig. 3B). The Pearson correlation coefficient was 0.068 ($P=0.244$).

A simple log transformation of an allometric model demonstrated ontogenetic differences in the slopes of the OS-FS relationship (Fig. 4). Slopes were significantly reduced for the newly hatched yolksac stage (I) and the larval flexion stage (IV). However, stage-I larvae were the same age; therefore variability due to ontogeny may be difficult to evaluate. Variability in fish length for stage-IV larvae may reflect subtle ontogenetic differences in caudal fin flexing and thus variation in the OS-FS relationship (Table 3).



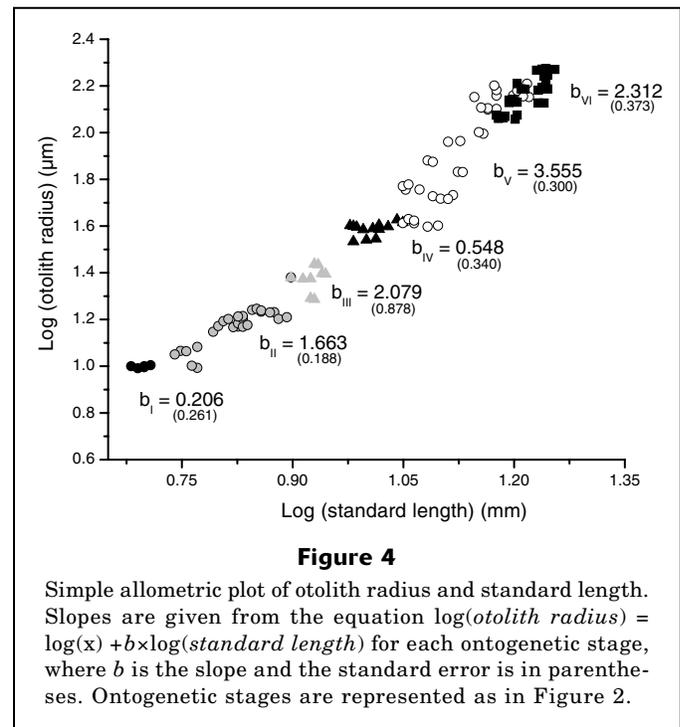
Comparison of the TVG, BI, and MF models

To account for ontogenetic change in the OS-FS relationship, we applied the BI model separately for pre-flexion and postflexion larvae. Mean back-calculated size-at-age for the TVG model varied from -10.3% to $+0.93\%$ of the observed mean-length-at-age and consistently underestimated size from 20 dah to 100 dah. The stage-specific BI model varied from -3.5% to $+6.4\%$, centering closely around zero, and the MF model varied from $+2.4\%$ to $+13.1\%$ and consistently overestimated size from 15 dah to 100 dah (Table 4; Fig. 5). These results indicate that the ontogenetic stage-specific BI model more accurately describes the observed mean size-at-age trajectories for delta smelt. However, the observed size-at-age was variable from 50 dah to 100 dah, resulting in statistically reasonable fits for all the models, with r^2 values ranging from 0.994 to 0.935 (Table 4).

Discussion

Validation of daily otolith increment formation

Accurate size-at-age estimates are important for measuring subtle differences in growth during the early life history of fishes because they are used to examine factors affecting recruitment success for many species (Rice et al., 1987; Sirois and Dodson, 2000). However, variability in age estimates can occur. Much of this variability in age estimates depends largely on when



the first increment is estimated to have formed (Campana and Neilson, 1985; Campana, 2001). In this study, increment formation in laboratory-reared delta smelt began six dah, about the time of first feeding. Numerous studies of other smelt species have also revealed that

daily increments form at first feeding (Sepulveda, 1994; Hirose and Kawaguchi, 2001). However, for some species of smelt, increment formation does occur at hatching (Ohama, 1990). Otterlei et al. (2002) demonstrated that temperature could further increase age variability by altering the timing of the first increment depending upon when, in the season, a fish was born. Delta smelt spawn from late February through June, potentially resulting in cohorts experiencing temperature differences of more than 10°C at birth (Moyle, 2002). This temperature difference could result in up to a two-fold change in the embryonic development and lead to a 2–3 day difference

in the timing of first feeding for delta smelt (first author, unpubl. data).

Otolith-size–fish-size relationship

The results of this study showed that minimal age-independent variability occurred in the OS-FS relationship and that growth rate effects were negligible (Fig. 3, A and B). Removing the effect of age resulted in a strong correlation between otolith growth and fish growth, indicating that at the preflexion stage, otolith growth was proportional to somatic growth. However, the OS-FS relationship showed a significant interruption in linear growth due to an ontogenetic shift at the postflexion stage, thus demonstrating that the assumption of constant proportionality was violated (Fig. 4). Moreover, this change in proportionality corresponded with the transition from preflexion larvae to postflexion-stage juveniles. Several studies, across broad taxonomic orders have demonstrated similar deviations from proportionality in the OS-FS relationship (e.g., flatfish (*Rhombosolea tapirina* and *Ammotretis rostratus*) [Jenkins, 1987], rainbow smelt (*Osmerus mordax*) [Sirois et al., 1998], and Atlantic cod (*Gadus morhua*) [Otterlei et al., 2002]), which were also associated with life-stage transitions.

Measured growth-rate effects were weak for delta smelt (Fig. 3B) and, thus, are not likely to further explain the age-independent variability in the OS-FS relationship. In contrast, Sirois et al. (1998), found significant growth-rate effects in the OS-FS relationship for rainbow smelt. Furthermore, Hare and Cowen (1995) found both growth-rate effects and ontogenetic shifts in the OS-FS relationship for bluefish larvae (*Pomatomus saltatrix*). These studies highlight the different mechanisms responsible for the variability in the otolith and somatic growth relationship, and, thus, potential violations in the constant assumed proportionality for linear back-calculation models.

Other factors that can influence the OS-FS relationship include temperature and salinity. In the field, delta smelt can experience a broad range of temperatures during their larval stage. The effects of differing temperatures at this life stage on the OS-FS relationship and the influence on otolith back-calculations from field-caught fish is unknown. It is assumed that otolith growth is allometric to fish growth during seasonally variable temperatures. For our study, delta smelt were reared in temperature and salinity controlled conditions, and therefore temperature and salinity were considered to have negligible effects and did not influence the variability in the OS-FS relationship. However, temperature variability can result in different

Table 4

Comparison of growth curves generated from otolith size-at-age data. r^2 = coefficient of determination for estimates of size-at-age and known size-at-age for each age group. “% range of mean size-at-capture” represents the variability between estimated size and known mean size at time of sampling.

Model	r^2	% range of mean size at capture
Biological intercept	0.994	–3.5 to +6.4
Modified Fry	0.935	+2.4 to +13.1
Time-varying growth	0.038	–10.3 to +0.90

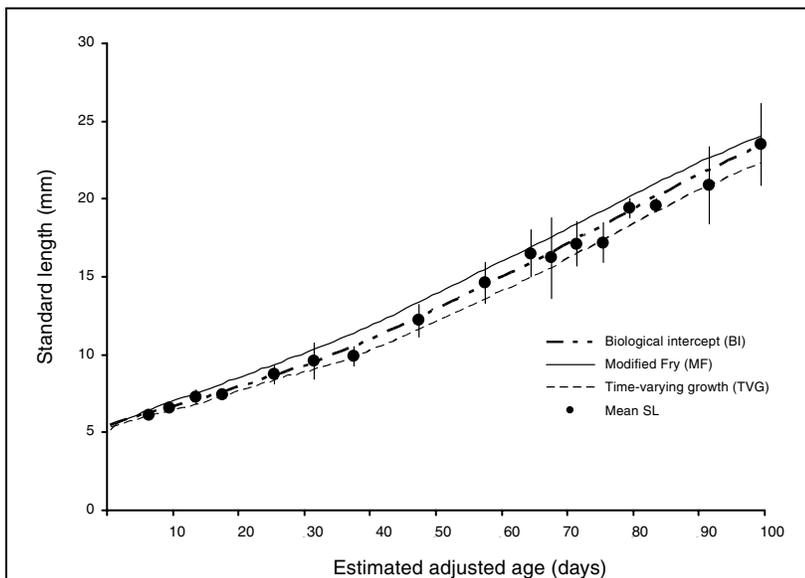


Figure 5

Growth curves back-calculated from delta smelt (*Hypomesus transpacificus*) otoliths. Size-at-age data for laboratory-reared fish are shown as points with ± 1 standard deviation. Three models of back-calculation were used to generate growth curves from otoliths: the modified Fry (MF), the stage-specific biological intercept (BI), and the time-varying growth (TVG) model.

OS-FS relationships and inaccurate size back-calculations. Indeed, Otterlei et al. (2002) found significant differences in the OS-FS relationships for Atlantic cod reared at different temperatures and therefore temperature effects can result in biased back-calculations if not considered in back-calculation procedures.

Despite the strong correlation between otolith and somatic growth during the preflexion stage, a significant shift in this relationship occurred during caudal fin flexing in the juvenile stage. This morphological transition signals a deviation from constant proportionality in the OS-FS relationship for delta smelt. Therefore, the appropriate choice of a back-calculation model will depend on the form of the relationship between otolith size and fish size. Incorrect assumptions regarding the shape of the OS-FS relationship in various back-calculation models may cause errors in back-calculation of size-at-age and the predictability of growth rates (Hare and Cowen, 1995; Otterlei et al., 2002). Campana (1990) suggested the use of a stage-specific form of the BI model to account for the ontogenetic shifts in the OS-FS relationship.

Comparison of the TVG and MF model with the stage-specific BI model

The ontogenetic stage-specific BI model used in our study provided the most parsimonious size-at-age estimates. The TVG consistently underestimated size-at-age, whereas the MF model over-estimated size-at-age for fish greater than 30–40 dah (Fig. 5). Estimated mean size-at-age for the stage-specific BI model was most similar to the observed size-at-age with the minimum and maximum percent deviation of individual size-at-age symmetrically distributed about the mean observed size-at-age. In contrast, the minimum and maximum percent deviation was negative for the TVG model and positive for the MF model (Table 4).

Unlike the stage-specific BI model, the TVG and MF models did not accurately estimate size-at-age because of ontogenetic shifts in the OS-FS relationships. The TVG model was developed to compensate for growth-rate effects in the OS-FS relationship (Sirois et al., 1998). However, for reared delta smelt, growth rate effects in the OS-FS relationship were minimal. When growth-rate effects are negligible, the results of the TVG and the nonstage-specific BI model should be identical (Sirois et al., 1998). This study demonstrates that when ontogenetic shifts occur in the OS-FS relationship independent of growth-rate effects, the TVG model may give poor estimates of size-at-age. Moreover, Vigliola et al. (2000) found the MF model accurately estimated size-at-age for three species of *Diplodus* (seabream), because of the allometric OS-FS relationship. However, for delta smelt, the simple allometric relationship of the MF model consistently resulted in an overestimation of size-at-age because of an ontogenetic shift in the OS-FS relationship.

The transition from the preflexion larval stage to the postflexion juvenile stage created difficulties for accurately estimating size-at-age for both the TVG and MF

models. Owing to the unique ontogenetic shift in the OS-FS relationship that delta smelt undergo, the stage-specific BI model more accurately estimated fish size-at-age. However, because of the variability in observed length-at-age, each model described population growth rates with a high degree of certainty (all r^2 values were greater than 0.93). Therefore, we argue that caution should be taken when describing patterns in hatchery-reared growth rates because measured growth rates in our study were significantly reduced in comparison to field growth rates (first author, unpubl. data). Finally, although the intercepts for the stage-specific BI model were derived from the mean population life-stage transition (12 mm SL), the size at life-stage transitions for individuals can be variable, resulting in complex individual biological intercepts that were not taken into consideration.

Conclusions

Criteria for choice of growth back-calculation models

The recent interest in back-calculated size-at-age for individual fish based on otolith increments has resulted in the development of numerous methods to back-calculate size-at-age. The choice of various back-calculation methods can be difficult because assumptions underlying each model may not be evaluated completely. To guide the proper choice of back-calculation models, we recommend a critical examination of the OS-FS relationship. Furthermore, the assessment of ontogenetic variability and growth effects (i.e., Hare and Cowan, 1995) should be evaluated prior to choosing a model. Application of back-calculation techniques requires validation of otolith growth and somatic growth relationships for each species. Therefore, validation may even need to be conducted on a species- or stock-specific basis, and at various levels of environmental variability (see Otterlei et al., 2002). Moreover, accounting for ontogenetic and growth effects on the proportionality of otolith size to fish size will help guide the development and application of appropriate back-calculation models and will lead to accurate estimates of size-at-age for fish recruitment studies. Thus, we conclude that the modified BI model will allow for an accurate estimate of growth histories and reliable information for determining factors influencing delta smelt recruitment.

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